WILLIAM A. CANNON
THE SONORAN DESERT'S FIRST RESIDENT ECOLOGIST

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ABSTRACT

William Austin Cannon (1870–1958) was the first resident investigator at the Carnegie Institution of Washington's new Desert Laboratory in Tucson, AZ. He pioneered in the physiological ecology of desert plants and in the study of root systems, particularly the effects of oxygen and temperature on root growth. He also held a worldwide interest in desert ecosystems. Well-known during his lifetime, he has since been largely forgotten.

"Dr. W. A. Cannon has been selected as resident investigator of the Desert Botanical Laboratory of the Carnegie Institution," read the anonymous notice in the *Botanical Gazette* for February 1903.[1] Six months later, Cannon (Fig. 1) arrived in Tucson, then a small desert town of 7500. The recently erected laboratory building stood halfway up Tumamoc Hill two miles west of downtown Tucson. The laboratory grounds included more than 800 acres of surrounding desert.

This unique establishment owed its existence to the farsightedness of Frederick V. Coville, curator of the U.S. National Herbarium, who, during his exploration of Death Valley in 1891, had been impressed by the adaptations of desert plants to their harsh environment. Clearly, the desert was a unique and little-known ecosystem; equally clearly, what was needed was a research station devoted to desert investigations. When he presented this idea to the botanical advisory committee of the Carnegie Institution of Washington, they not only concurred, they provided $8000 to construct a building, furnish laboratory equipment and pay the salary of a resident investigator for one year.[2] Coville and Daniel T. MacDougal, director of laboratories at the New York Botanical Garden, then toured the Southwest to find the most suitable site and selected Tucson because, among other advantages, it was accessible by rail and located in undisturbed desert.

Both Coville and MacDougal were already well-established scientists and doubtless neither cared to assume the post of resident investigator for a yearly salary of about $2000 plus $25 a month for out-of-pocket expenses. They selected William Cannon, and by 1 September 1903, he was on the spot, the Sonoran Desert's first resident ecologist.

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FIG. 1. William A. Cannon (1906). Courtesy of Arizona Historical Society.

Cannon, then thirty-three, had been MacDougal's assistant at the New York Botanical Garden, where he investigated the anatomy of plant hybrids (Cannon 1902a, 1903a, b, 1904a). A late bloomer, he had earned his bachelor's degree at twenty-eight, his doctorate at Columbia University at thirty-one. While working towards a master's degree at Stanford University, he had considered such divergent botanical subjects as redwoods and giant kelp, turning his mind to the plant geography of one and the evolutionary ecology of the other (Cannon 1901a, b). He was already accustomed to thinking like an ecologist, then, when MacDougal offered him the job of resident investigator.

The new Desert Laboratory was devoted to ecology before the very word was widely used. Like most of his ecological contemporaries—Henry Gleason, Frederic Clements, Henry Cowles, Frederick Coville, Edgar Transeau, Forrest Shreve—Cannon had a foot in two worlds: traditional botany, especially anatomy and morphology, and the budding field of plant ecology.[3] His interest in plant ecology thrived at the Desert Laboratory, and in 1915 he became one of 268 charter members of the Ecological Society of America, along with Shreve and MacDougal (Burgess 1977).

Cannon started work with instructions to inquire into the "morphology, physiology, habit, and general life-history of the species indigenous to the deserts of North America" (MacDougal 1903, p.

249). As he settled in, he could envision enough research ahead to keep him busy a long time, and he was, he told MacDougal, very much pleased with the prospect.[4]

First, however, he had to supervise completion of the laboratory. The interior still lacked woodwork, floors, and wiring. The gasoline-powered pump for the water system needed to be inspected and the new road up Tumamoc Hill required substantial improvement. Bills had to be settled, equipment installed, botanical textbooks and manuals purchased, and the corners of the property located. Also, installation of a telephone was mired in local politics. Finally, after two months of nagging contractors and tying up loose ends, Cannon was able to notify MacDougal that "the contractors should be out of this building and we in before the end of the week."[5]

Ready to begin research at last, he selected *Fouquieria splendens* as his first subject because "it responds so delicately to its surroundings." Someone had told him that "a very little encouragement in the way of rain in the summer is sufficient to make it send out . . . leaves . . . in a surprisingly short time."[6] He planned to study its anatomy first, then its root system and physiology. Soon, under prodding from MacDougal, he agreed to study "some fleshy form," too, and selected *Ferocactus wislizenii.*

Cutting cross-sections of *Fouquieria* stems for anatomical study proved surprisingly difficult, but Cannon substituted ingenuity for the more usual microtome. By softening the tissues in glycerine first, then sawing at the stems with two different razor blades, he managed to obtain adequate material. Before the year was out, he also studied *Ferocactus* anatomy, measured transpiration of *Mammillaria microcarpa,* determined the water content of a full-grown *Ferocactus,* and measured diameter changes in *Ferocactus* and *Carnegiea gigantea.* He was, apparently, the first scientist to suggest that columnar cacti "must undergo considerable seasonal and daily change in diameter owing chiefly to alterations in temperature and water supply, and that if they did, the corrugations would come in very neatly in permitting the adaptations to these variations."[7]

Meanwhile, Volney M. Spalding, an elderly botany professor from the University of Michigan, had become the Desert Laboratory's first visiting investigator. When he arrived in December 1903, he found Cannon devising a novel method for measuring transpiration according to some suggestions MacDougal had made. Cannon helped the older gentleman settle in and told MacDougal, "He is a continual inspiration[,] . . . a good one to set the ball rolling."[8] The innumerable opportunities for research must have seemed overwhelming at first, and Cannon welcomed Spalding's steadying influence and botanical knowledge. With assistance and advice from Spalding, then, Cannon continued to refine his transpiration-measuring apparatus.

Physiologists then measured transpiration by three different methods, none of which could be used on living plants in situ. Cannon ingeniously skirted this difficulty by devising a portable apparatus. His method had the further advantage of being noninjurious, therefore suitable for repeated measurements on the same plant over days or weeks (Cannon 1905a). Basically, he created an airtight compartment by pouring a cement slab under a plant and setting a bell jar over both plant and slab. Before sealing the jar in place, he put a hygrometer and a thermometer inside. The change in absolute humidity over a period of time, calculated from relative humidity and temperature, equaled the amount of vapor transpired by the plant (Cannon 1905a).

In spite of certain drawbacks, this method worked well enough that in one year he measured the transpiration of *Carnegiea, Larrea tridentata, Encelia farinosa,* and *Fouquieria,* collecting the first data on transpiration in desert plants. In fact, his investigation of *Fouquieria* transpiration (Cannon 1905b) was among the earliest physiological studies of North American xerophytes. (The first, Spalding's 1904 study of *Larrea,* relied partly on transpiration data that Cannon had gathered.)

Although transpiration work must have filled much of 1904 (by May he had made more than seventy-five measurements), he also studied *Phoradendron* germination with special emphasis on how seeds penetrate their host (Cannon 1904b); visited the San Francisco Peaks in northern Arizona (Cannon 1906a); and excavated root systems of *Ferocactus, Larrea, Carnegiea,* and other desert plants.

As Cannon studied the adjustment of plants to their desert environment, he himself adjusted to his still unfamiliar surroundings. An unseasonably heavy rainfall in May stimulated new leaves on *Fouquieria* and *Larrea,* and he told MacDougal that he was "looking for a spring growth of annuals but thus far none have appeared."[9] None *did* appear, of course, until the following February, when good winter rains made the desert "a veritable paradise."[10] When he first arrived, the weather had been unusually cool for September, and he was quite willing to "wait another year before experiencing the hottest weather Tucson can put up."[11] When this came to pass the following June, he said that "even the most hardened liar among the natives will hardly defend this summer climate."[12] The weather held yet more surprises. In mid-August, when he returned from his trip to the San Francisco Peaks, he found "quite another country from the desert that we had left a little over two weeks before"[13] as lifeless shrubs burst into leaf and flower in response to summer rains.

With the summer came visiting investigators whose academic calendars freed them for three months of research. They included Francis Lloyd, a plant anatomist from Columbia University, and Burton Livingston, a plant physiologist associated with the University of Chicago. Cannon helped them settle in and rounded up suitable apparatus for their experiments. Another visitor that summer was Coville, whose surprise visit satisfied him that everything was "in first rate shape, including enthusiasm and progress."[14] Cannon welcomed the influx of visitors. There was no lack of research problems to keep them all busy; as he told MacDougal, their main difficulty was "to choose wisely from the abundance."[15]

As resident investigator, Cannon bore the particular responsibility of justifying the Carnegie Institution's initial investment. The Desert Laboratory had been founded on a provisional basis, and its funding was appropriated year by year. If, after its first five years, it showed sufficient promise, it was to become a permanent research station (Bowers 1990). Before the lab was a year old, Coville let Cannon know that "we are looking for a fine large paper from you. The future of the laboratory will be much influenced by the character of this paper and by the discoveries it contains."[16]

The future arrived two years before the end of the probationary period. After Institution president Robert Woodward visited in July 1905, he proposed to greatly enlarge the scope of the laboratory by increasing the work force, constructing staff residences, and remodeling the building. Best of all, he wanted to make the Desert Laboratory a permanent station as soon as possible. This was, as MacDougal told Cannon, "immensely gratifying. . . . it is very pleasing indeed to know that the things you are doing are being appreciated in this way."[17]

MacDougal was appointed director of the Desert Laboratory effective 1 January 1906, and immediately began to enlarge his staff. Cannon was kept on, and, to his delight, Spalding, Lloyd, and Livingston were added to the roster of staff scientists. "They all have had considerable experience here and will come with good conceptions of the extent as well as the nature of the work to be undertaken," he told MacDougal.[18]

Shortly thereafter, Cannon published a popular article about the Desert Laboratory (Cannon 1906c), a kind of manifesto for the nascent field of plant ecology. Desert Laboratory scientists, Cannon noted, "reach out in two directions: they endeavor to record as fully as possible the environmental factors which surround and which influence every day the plants of the desert, and they endeavor to note and to measure as fully and as accurately as possible the reactions of these plants to these stimuli" (Cannon 1906, pp. 30–31). He listed problems that confront the desert biologist: how do desert conditions differ from those in humid areas? how do endemic plants react to these conditions? where did desert plants come from? how and when did they become adapted to the desert?

With the continuity of the Desert Laboratory assured, the staff initiated an extraordinary range of research projects (Bowers 1990). Spalding set up nineteen permanent plots on the Desert Laboratory grounds and mapped the vegetation of each. MacDougal monitored plant succession at the recently formed Salton Sea and undertook a series of experiments aimed at elucidating the mechanisms of inheritance. Forrest Shreve, who joined the staff in 1908, examined establishment of desert perennials and frost tolerance of *Carnegiea.* Livingston continued his work on evaporation and transpiration. Plant physiologist Herman Spoehr concentrated on photosynthesis. Lloyd continued his anatomical studies.

Several years earlier, the president of the Carnegie Institution had worried that Desert Laboratory researchers, working in close proximity on similar problems, would infringe on one another's scientific territory. He had even asked if Cannon had any objection to assisting summer investigators, since "they might possibly take undue advantage of the knowledge they may gain from you and anticipate you in the publication of important results."[19] Cannon had promptly replied that "the ground for work here is so broad that several botanists could work at one time not only without 'jumping' each other's claim but to their great mutual advantage."[20]

True as this was then, Woodward's forbodings acquired substance before too long. There is, as Paul B. Sears noted in another context, an ecology of ecologists (Sears 1956). Just as coexisting animal species create unique niches by partitioning available resources, so coexisting ecologists partition the field of research. At first, as Cannon had indicated, the need for partitioning hardly existed. As more researchers arrived, however, division of research opportunities inevitably (and probably unconsciously) took place. With Livingston concentrating on transpiration and the physical environment, Lloyd on anatomy, Spalding (and later Shreve) on vegetation and plant geography, and MacDougal on anything that took his fancy, Cannon had little choice but to narrow his field of research. Although he continued his anatomical and ecological studies for a few more years—between 1906 and 1908, he examined the distribution of chlorophyll in nineteen species of desert plants (Cannon 1908a), measured salt concentration in the sap of halophytes (Cannon 1908b), and studied inheritance in plant hybrids (Cannon 1908c, 1909a)—after 1908 he specialized in roots.

Begun as one among many lines of research, these root investigations proved "wonderfully enticing,"[21] and between 1909 and 1954 he published some two dozen papers on the subject. In 1909, the study of root systems was virtually untouched,[22] as Cannon noted: "The character and extent of the root systems of desert plants, as well as the role which they play in the distribution of these plants, are in the main not known." He recommended investigating roots in relation to soil moisture, temperature, oxygen, and adjacent plants. "The influence of these and other factors on the presence of plants in their peculiar habitats are among the most pressing problems of desert botany that await studious inquiry," he wrote (Cannon 1909b, p. 59). With these words he mapped out enough research to fill the next forty-five years.

He quickly made several novel discoveries: that the roots of seedling *Opuntia versicolor* act as water storage organs (Carnegie Yearbook 1906); that *Orthocarpus purpurascens* was a root parasite on at least eighteen different hosts (Cannon 1909c); that *Krameria grayi* was also parasitic (Cannon 1910a); and that certain desert shrubs produce ephemeral rootlets to take maximum advantage of brief rainy periods (Cannon 1912a). He posited that the shallow roots characteristic of cacti went hand in hand with their succulence; since the upper soil layers dry out quickly, "plants depending on this stratum for moisture must either be short-lived or have the capacity of storing up water against the period of drought" (Cannon 1913, p. 420; see also Cannon 1909b).

In 1911 he summarized his first five years of root research in the classic *Root Habits of Desert Plants.* His ultimate goal, he wrote, was to conduct root studies on "broad physiological-ecological grounds," which to him meant primarily experimental work. First, however, he required exact descriptions of root systems, therefore he undertook "the prosaic work of excavating" (Cannon 1911, p. 10). He dug up annuals with roots intact; perennials he studied in place, first removing the soil, then fixing a grid of measuring tapes above the exposed roots and drawing them to scale.[23] After examining the roots of twenty-one desert perennials and thirty-six summer and winter annuals, Cannon stated conclusively that, contrary to the widespread belief that the roots of desert plants were uniformly deep, they were instead "extremely variable as regards depth of penetration, lateral extent, and other characteristics, and . . . no one type of root can be said to be the prevalent one" (Cannon 1911, p. 8). He grouped desert root systems into one generalized and two specialized types. Plants with generalized root systems showed good development of both tap and lateral roots, he said. Most desert perennials belonged to this category. Specialized root systems featured either deep tap roots or shallow laterals. The heteromorphic root systems typical of cacti possessed both an anchoring portion and an absorbing one (Carnegie Yearbook 1910).[24]

Although most interested in root physiology, Cannon did discover many interesting ecological relationships as he excavated. When he found that the root system of one *Larrea* was penetrated by roots from sixty others, he commented that "competition between neighboring *Covillea* [*Larrea*] on the bajada, for soil water, is presumably keen" (Cannon 1911, p. 61). If near neighbors belonged to different species, however, no direct competition for water ensued, since their roots occupied horizontal layers at different depths (Carnegie Yearbook 1909).[25] His ideas about competition contradicted those of

Shreve, who categorically denied the existence of competition in desert plant communities (Shreve 1911, 1915, 1917, 1936).[26]

Cannon deduced that "plants having roots which reach to greater depths than 15 cm. can obtain some moisture at all seasons," whereas shallower roots could absorb water only after rains. Seedlings, in order to survive, "must send their roots below 15 cm. within six weeks following the close of a stormy period" (Cannon 1911, pp. 16–17).

He saw a close relationship between root type and plant distribution: plants with prominent tap roots required deep soil and would be limited in their distribution, while those with generalized roots could grow in a variety of habitats and would be broadly distributed. This was a point he reiterated many times (Cannon 1906b, 1911, 1913a, b, 1915a, 1925a); evidently he seldom thought to look for aboveground determinants of plant distribution.

Starting in 1907, Cannon spent part of each year on the California coast. This was the result of the Carnegie Institution's support of plant breeder Luther Burbank, stationed in Santa Rosa, CA. Cannon, by virtue of his background in cytology, was asked to make cytological and histological examinations of Burbank's hybrids (Cannon 1908c, 1909a). He set up temporary headquarters at the Hopkins Seaside Laboratory in Pacific Grove, but before the summer was over, officers of the Carmel Development Corporation offered to provide a permanent site—three acres of land and a new laboratory building in Carmel-by-the-Sea. MacDougal liked the idea immensely; a seaside laboratory would be a refreshing retreat from Tucson summers, and it would "give the administration the idea that we are being appreciated."[27] The institution approved the plan in December 1908, and the following summer, the Coastal Laboratory was ready for occupancy.

At the new laboratory Cannon was at first relegated to the role of MacDougal's research assistant, reporting on the growth and survival of transplants in the experimental garden. Eventually, as MacDougal spent more time at the Coastal Laboratory, Cannon was freed to undertake his own research once again and to make excursions to nearby points of botanical interest—the endemic groves of *Pinus radiata* on the Monterey peninsula, for example, or the populations of *Abies bracteata,* another endemic, in the Santa Lucia Mountains. These trips often combined his dual interests in plant ecology and root systems. After the chaparral understory was cleared from *P. radiata* groves, he noticed, the pines died within two years. He speculated that, once its protective cover was removed, the soil dried out during the long, rainless summers, and the pines died of drought (Cannon 1913d). He discovered that *Quercus agrifolia,* characterized by extensive feeder roots, was "wholly dependent upon the water coming directly from the rains or . . . run-off," and "for this reason, the roots of adjacent trees compete . . . in a manner exactly comparable to desert shrubs. Thus it follows that, because of a relative paucity of water, the trees come to have an open stand" (Cannon 1914b, p. 423). This was also true of *Q. douglasii* but not of the deeply rooted *Q. lobata,* a floodplain species.

Having launched the Coastal Laboratory, Cannon promptly left it for a trip to the Algerian Sahara. The reason for this journey is not entirely clear. Possibly MacDougal, who never lacked for big ideas, suggested it; he told one correspondent that Cannon was "having a most profitable time in extending some of our lines of work here into the Sahara." In fact, he added, he expected similar developments for many of their research projects.[28] Cannon's official reason for his Saharan trip was to "examine the more obvious features of the physiological conditions prevalent in the region . . . and, in connection with these observations, to make some detailed studies of the root-habits of the most striking species of the native flora" (Cannon 1913b, p. 1). For whatever reason, Cannon left for Algeria via London and Brussels in April 1910.

Arriving in Algiers in October, he traveled across the Atlas Mountains and into the Sahara, a round trip of 1000 miles by horse-drawn carriage, motorcycle, and camel. In February he traveled up the Nile to Aswan, then returned to Algeria, where he made Biskra his headquarters for a month of local excursions. In April he left for Europe, and by the middle of May he had written a substantial proportion of *Botanical Features of the Algerian Sahara* (Cannon 1913b).

During his Algerian sojourn, he excavated the roots of sixteen species and conducted seven "censuses" of vegetation in sixteen-meter-square plots.[29] Of more interest is the rich comparative material he gathered on desert environments. His knowledge of the Arizona desert gave him a unique perspective on the Algerian Sahara. Around Tucson, he said, warm-season rainfall promoted a rich succulent flora; farther west, where the rainy season was limited to the winter months, few succulents occurred. Similarly, in Algeria, where the single rainy season occurred during the winter, "the absence of plants with water-storage facilities" was a prominent feature of the vegetation (Cannon 1913b, p. 69).[30] In the extreme desert of the Algerian Sahara, plants struggled mainly with their environment and competition was negligible. Competition was readily apparent in regions that were not quite so arid, however, as in the vicinity of the Desert Laboratory.

He was startled by the enormous number of grazing animals in southern Algeria—nearly two million sheep, 588,000 goats, and 126,000 camels. Only the poisonous, distasteful, or well-armed plants escaped consumption, he noted. Again, his experience in Arizona, where plants were spinier than in Algeria but only lightly browsed, provided a fruitful comparison, and he concluded that the evolution of spininess had little to do with browsing animals (Cannon 1913b).

After Cannon returned to Tucson in September 1911, he devoted himself to experimental studies. In 1912 and 1913 he tackled the vertical placement of root systems with reference to soil moisture and aeration, then, in 1914 and 1915, in relation to soil temperature (Cannon 1913a, c, 1915a, 1916, 1917a, 1918; Cannon and Free 1917). He devised his own equipment for some of these experiments: a simple root-growth box, for instance, and more elaborate "thermostats," glass tubes in which roots could be held at constant temperatures or charged with oxygen, helium, or other gases. Between 1916 and 1918 he investigated the joint effects of temperature and aeration on root growth, varying the gaseous elements introduced into root systems. "I have run through one set of mesquite seedlings on a nitrogen diet and they came off unscathed," he reported. "But the opuntia I am now watching seems to behave quite differently, growth slowing very markedly."[31] By this time, the Coastal Laboratory had undergone extensive remodeling, and working there was, Cannon reported, "more fun than a goat."[32]

These methodical experiments made several novel contributions. He learned that unrelated species in the same habitat could react differently to soil temperature, as did *Fouquieria* and *Prosopis velutina* (Cannon 1915a). Cannon and soil scientist Edward Free were the first to point out that response to soil oxygen was also species-specific and that species could vary widely in their oxygen requirements (Cannon and Free 1917). Cannon demonstrated that roots of cacti cannot extract water from cold soils, thus "in regions where cacti are abundant, either native or introduced, rains occur during the warm season" (Cannon 1916, p. 441; see also Cannon 1915a, 1925a). He defined a root-growth index, TR, that was "the summation of root growth at the temperatures employed" (Cannon 1918, p. 64); he noted that when a species is limited in distribution by unfavorable temperatures, TR should be small at the edge of its range and large in the center. He even suggested that TR could be plotted as isolines, thus showing the relation between root temperature and distribution.

These experiments emphasized artificial systems that examined a single parameter at a time. As one plant physiologist recently pointed out, such studies leave "a void in understanding the mechanisms regulating root development in natural environments" (Feldman 1988, p. 618). Cannon evidently never noticed this limitation in his work. He criticized Weaver's *Ecological Relations of Roots* (Weaver 1919) for failing to identify soil temperature and soil aeration as potential limiting factors in root development (Cannon 1920), yet he himself failed to consider myriad other aspects of root development such as genetic constraints, hormonal control, soil strength, geotropism, and root exudates.

"Cannon is still bent on going to Australia and asserts that he has discovered no conditions which would in any way impede his movements," MacDougal told a friend in July 1917.[33] Having already cancelled a trip to southern Europe and Palestine, Cannon was evidently determined that U.S. involvement in the war would not interfere with his plans a second time, and he prevailed upon MacDougal to write a letter to the State Department assuring them that the proposed trip was "imperative." MacDougal obliged, and in April 1918 Cannon was on his way with the Carnegie Institution's permission to work at his own expense for one year while drawing his regular salary.

Within a month of his arrival in Sydney, he had surveyed the country around Oodnadatta, a "sure enough desert," and drawn up plans for fieldwork: "After working over the 'Mulga' zone, which should furnish much of interest, and of course after seeing this region, I will go west of Port Augusta into the 'Mallee' zone and study its characteristics. These two, with the desert, should make a good story."[34] By the middle of August he had collected some 100 herbarium specimens, taken "a splendid series of photographs of habitats and plant habits," and amassed a "considerable body of notes." If not for the war, he told MacDougal, he would request an extension of his leave because "problems and new points of view are opening up constantly."[35]

Cannon's experience in South Australia reinforced his earlier impression that season, timing, and amount of rainfall were paramount in determining the vegetation of arid regions. "So far as the well-being of the vegetation is concerned," he wrote, "the reliability of the rains . . . is of capital importance. And in a general way the reliability of the rains decreases with the decrease in the amount of rainfall, which it will be seen only serves to intensify the effects of progressive aridity" (Cannon 1921, p. 8). Using five years of rainfall data from six different stations, he estimated that the ecologically effective rainfall would be 0.15 inch or more and that the percentage of noneffective rainfall would rise as the yearly total precipitation decreased.[36]

As in Algeria, he examined root systems when the opportunity arose. He discovered that, in very dry regions, "the limit of root penetration may coincide with the depth of the penetration of the rains. . . . For this reason, in regions where the general penetration of the rains is slight, the placing of the roots of perennials is necessarily superficial" (Cannon 1921, p. 137). Weaver (1926) later corroborated this point.

While in Australia, Cannon largely set aside his experimental predilections and functioned more as ecologist than physiologist. He noted that the various trees and shrubs all bore a "xerophytic stamp," but despite their superficial monotony, they showed "a bewildering variety of adjustments" to their arid environment (Cannon 1921, p. 1). Perennials tended to develop markedly long leaves that, in the case of *Acacia,* were actually phyllodes. He hypothesized that the length-to-width and area-to-length ratios of leaves and phyllodes could be used as an index of their xerophily. In mesophytic leaves in general, the ratio of area to length was 40:1, but among South Australia plants, it was roughly 5:1, an indication of how aridity had selected for leaves with smaller transpirational surfaces.[37] Phyllodes could be up to twenty-four times longer than wide, which again showed adaptation to the unfavorable water supply. Other water-saving features of leaves included hairs, resinous secretions, heavy cuticles, and sclerenchymous tissue.[38]

Cannon wrote the first draft of *Plant Habits and Habitats in the Arid Portions of South Australia* on the homeward journey while his experiences were still fresh in his mind. The book shows him to good advantage as a physiological ecologist whose interests were not bounded by laboratory walls. Field studies complement experimental work, he wrote, and although "it has not been practicable to carry out direct experiments on subjects suggested by the observations, it has been of interest and profit to interpret the observations so far as possible in the light of experimental results already accomplished" (Cannon 1921, p. 2).

When Cannon came home in May 1919, he resumed root experimentation at the Coastal Laboratory, now his research home. He also made plans for a year-long stay in South Africa, and, despite difficulties in obtaining funds from the Carnegie Institution, left for Pretoria in the spring of 1921. Through the courtesy of Pole Evans, a South African botanist, he was given a first-class rail pass, and the Botanical Survey of South Africa offered to pay the remainder of his traveling expenses. His itinerary allowed for brief stays in the Little Karroo, the High and Low veldts, and the Namib, and a prolonged sojourn in the Central Karroo.

Cannon embarked on this trip primed with his knowledge of arid regions on three continents. Each region presented its own problems which required specific study: "even the common fact of aridity is exceedingly complex, possibly with unlike causes and characteristics as well as with dissimilar physiological and ecological relations" (1924a, p. 7). The flora and vegetation of each region were also distinct, and even a single genus, *Acacia* for example, did not behave uniformly from one desert to another. He found it impossible to outline a set of traits that would distinguish between plants of arid and semiarid regions. Although certain features were common to virtually all arid-adapted plants (recessed stomates, trichomes, reduced leaves, double epidermis, heavy cuticles),[39] there was no morphological type that was completely "eremological," that is, limited to arid lands. (Oppenheimer confirmed this point: "If true xerophytes are not all xeromorphous, conversely xeromorphous plants are not all xerophytes" [Oppenheimer 1960, p. 106].)

Structural adaptations to aridity had long interested Cannon. As early as 1908, he had noted that leaflessness and reduced leaves enable desert plants to lessen their transpiring surface. Certain species oriented their branches to protect leaves from intense midday illumination. Cannon had concluded that many xeromorphic characters could hardly "be attributed to the molding influence of the environment; it will doubtless be necessary to take into consideration the peculiar history of each plant, its gradual modification from its remote mesophytic ancestor, before habits and structure are satisfactorily related" (Cannon 1908a, p. 4).

Sixteen years later, after working in deserts around the world, he was ready to do just that—relate structure, evolution, and habitat. Two kinds of forces—heredity and the immediate environment—determined anatomical structure, he said (Cannon 1924a). Physiologists, often little accustomed to extremely arid regions, tended to stress environment in their studies of desert plants. He attempted to redress this imbalance by comparing the anatomy of arid-adapted plants with that of mesophytic relatives. Xerophytes had followed "very diverse morphological roads . . . during the long processes of adjustment" to aridity, he concluded (1924a, p. 110). Such xerophytic features as thick cell walls and well-developed sclerenchyma were "in part a modification of family structures by reason of which . . . survival is accomplished" (1924a, p. 120).

His comparative studies of arid regions led him to point out convergent evolution (although he did not use this term) in desert plants. Although, he wrote, desert perennials in general showed a marked diversity in growth-form, "species belonging to different genera, and even of different families, may be strikingly alike, although superficially so" (1924a, p. 155). Examples included the African genus *Aloe* and the American one *Agave,* and certain African species of *Euphorbia* and American *Echinocereus.* In the course of evolution, he explained, "species react to . . . common impinging environmental factors. Where reactions take fairly parallel courses, the results are to a certain degree harmonious, and to the degree that they are so the species tend to become more and more alike" (1924a, p. 158).

Cannon described *General and Physiological Features of the Vegetation of the More Arid Portions of Southern Africa* as the third of a series in his "minor research." The series itself, occasional papers on the botanical features of arid regions, was eventually to culminate in "a physiological–ecological work of a comprehensive nature on deserts in general" (1924a, p. 7). This ambitious work never came to pass; upon his return from South Africa, Cannon immersed himself once again in experimental studies of roots.

These root investigations, too, were to be initial steps in a more ambitious program: according to Cannon, "the ultimate aim of the investigations is to acquire data which will define as clearly as may be practicable the role played by the root in the activities of the plant as a whole" (Carnegie Yearbook 1922–1923, pp. 56–57). In *Physiological Features of Roots,* a monograph that summarized his numerous experiments, he presented a more detailed outline of his research goals. "Investigations should be carried out on the mutual relation of root and of shoot, particularly with reference to the effect on root-growth," he wrote (Cannon 1925a, p. 11). He recommended investigations of respiration in healthy and diseased roots, of gas exhange in roots, of translocation of oxygen from shoot to root, of root behavior with reference to soil microorganisms, and of enzymatic activities associated with root growth. In short, a comprehensive program would "comprise several phases of the physiology and ecology of roots, particularly those related to roots as reactive organs of plants" (Cannon 1925a, p. 12). Here again the broader studies never came to fruition; his tendency to examine every aspect of a given problem made for halting progress toward his larger goals.

Nevertheless he chipped away at this comprehensive program until his retirement. Among his major conclusions were that root growth at different oxygen levels is strongly controlled by temperature (Cannon 1923, 1924a, 1925a, b);[40] that there is often a close relation between "the degree of aerobism of a species" and its occurrence in a given habitat (Cannon 1925a, p. 167); that roots could obtain their oxygen supply from one of several sources—directly from the atmosphere, from gases dissolved in soil water or from byproducts of photosynthesis (Cannon 1932a, b, 1940). Continuing his cactus studies, he learned that "roots of *Opuntia* are exceedingly plastic and are directly affected by the immediate condition of the soil environment" (Cannon 1925a, p. 112), and once again confirmed experimentally that cacti are mainly restricted to regions of summer rainfall because they cannot extract water from cool soils (Cannon 1925a).

During the twenties and thirties, Cannon broke new physiological ground. He was apparently the first to study rates of root growth under varying temperature and aeration regimes. He was unique in emphasizing root adjustment to local conditions, and in correlating habitat with specific oxygen requirements. While most of his colleagues concentrated on crops and agronomic aspects of root growth (Aung 1974), he experimented with native plants.

By 1923, Cannon felt he needed more extensive research facilities. He thought that Stanford University might cooperate with the Carnegie Institution in establishing and maintaining a laboratory especially designed for root experiments. G. J. Peirce, the Stanford plant physiologist, was interested in the idea, Cannon told MacDougal, and added, "I am certain that such a branch laboratory will do no harm to this Department and close contact with a strong department of botany as they have at Stanford may be of much use."[41]

MacDougal disagreed. "The Institution has no honorary or inactive memberships," he informed Cannon. Furthermore, he did not believe that the institution could be induced to fund a cooperative laboratory such as Cannon proposed.[42] Communication between the two men deteriorated from this point. MacDougal, pulling rank, told Cannon, "It would be advisable for you to devote your energy this year chiefly to finishing up the experimental and literary work on your experiments with roots. . . . The South African work might well go over [into next year] and be finished at your convenience."[43] Cannon acceded, but five months later he tendered his resignation, to be effective 31 December 1924.[44]

It is difficult now to reconstruct the exact cause of their dispute. Perhaps MacDougal regarded Cannon's attempt to set up a separate laboratory as insubordination, or he may have been angry with Cannon for not progressing more rapidly with his root research. In any case, Cannon evidently remained at the Coastal Laboratory into 1925, probably to see *Physiological Features of Roots* through publication. The following year he took up a position at Stanford as a lecturer in botany. Although no longer attached to either the Desert Laboratory or the Coastal Laboratory, he remained a research associate with the Carnegie Institution through 1934.[45]

Even this was apparently more than MacDougal could stomach, for he tried to force Cannon out of the institution entirely in 1926. Burton Livingston, their mutual friend, was against this move and said so to Forrest Shreve: "I regard Cannon's last publication [*Physiological Features of Roots,* in all likelihood] as just as good as anything that has ever come from the department. . . . In his earlier work on roots C. opened the field and stands very high in my estimation." Cannon had been with the Carnegie Institution longer than any other botany worker, Livingston pointed out, "and some valid reason for his being dropped ought to be given, something besides general incompetence, for we know that is not a reason in this case."[46]

During retirement, Cannon returned to his early interest in classification of root systems (Cannon 1949, 1954). "A system of classification should be helpful in comparing the root systems of genetically diverse plants growing in a single habitat as well as those of genetically uniform stock which differ because of unlike environmental conditions," he wrote (Cannon 1949, p. 542). His classification scheme, which described and illustrated six primary and four adventitious types of root systems, has been called a classic (Zobel 1975). Ludwig (1977) found it "simple and workable" and suggested only minor modifications to suit it to a more quantitative age.[47]

When he died on 16 January 1958, Cannon had been largely forgotten by ecologists and physiologists alike. No obituaries appeared in the major journals and even the Carnegie Institution failed to note his passing in its yearbook. In earlier years, he had been well-known in his field; from 1910 to 1944, he was starred in *American Men of Science,* an indication that his colleagues ranked him among the top 1000 scientists in the nation. Today his reputation in ecological circles has been eclipsed by Shreve's.[48] Had Cannon worked more extensively in North American deserts, his ecological work might be better known. Shreve, however, effectively pre-empted this niche, which may have been why Cannon pursued desert studies on other continents.

If being the Sonoran Desert's first resident ecologist were Cannon's only claim to fame, he would be worth remembering. As it happens, he was much more. He was one of the first ecologists to take laboratory methodology into the field. He designed and carried out some of the earliest physiological investigations of desert plants, essentially inventing for himself the science of physiological ecology. Cannon was the first plant ecologist to discuss competition in deserts and the first to demonstrate that cacti are most prevalent in regions of summer rainfall because their roots cannot absorb water from cold soils. Although Volkens, Kerner, and Schimper (Oppenheimer 1960) anticipated him in Old World deserts, Cannon was among the earliest plant ecologists to investigate xeromorphic adaptation in the American desert. Moreover, he seems to have been *the* first plant ecologist to evaluate the influence of family characters on xeromorphic life-forms. He pioneered not just in the ecology of desert root systems but in the root system as an object of botanical inquiry at many levels; as Livingston said, "C. opened up the field." As Cannon narrowed his field of interest from roots in general to roots in the laboratory, he continued to make novel and worthwhile contributions, chief among them the reciprocal effect of oxygen and temperature on root growth.

His career as a whole showed an alternating pattern of going wide and going deep, of ecological broadening and physiological delving. His major research, the root work, enabled him to burrow deeply into a narrow topic, and his minor research, desert plant ecology, let him dabble in the broader issues of speciation, diversity, and adaptation. Because his training made him most comfortable with experimental studies, his best work in ecology was always firmly grounded in physiology and anatomy. He thought of himself as a physiological ecologist (Cannon 1921); today we might be more likely to classify him as an ecological physiologist.

If, rather sadly, his relationship with MacDougal soured toward the end, his long association with the Carnegie Institution was, on the whole, profitable for both the institution and the man. As Cannon himself told MacDougal in 1905, "[The Desert Laboratory] will be one of the leading botanical stations in the world; I am proud to be an associate in the work."[49]

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NOTES

AHS—Daniel T. MacDougal Papers, Arizona Historical Society, Tucson.
SC—Desert Laboratory Papers, Special Collections, University of Arizona Library, Tucson.

[1] The name "Desert Botanical Laboratory" was quietly replaced with "Desert Laboratory" around 1908. No written explanation for the change has come to light.

[2] Wilder (1967), McGinnies (1981), McIntosh (1983), and Bowers (1990) provide more information about the founding and subsequent history of the Desert Laboratory.

[3] McIntosh (1976), Cittadino (1980) and Tobey (1981) document the early years of American plant ecology.

[4] W. A. Cannon to D. T. MacDougal, 21 Sep 1903, AHS.

[5] W. A. Cannon to D. T. MacDougal, 2 Nov 1903, AHS.

[6] W. A. Cannon to D. T. MacDougal, 23 Oct 1903, AHS.

[7] W. A. Cannon to D. T. MacDougal, 10 Dec 1903, AHS. Cannon later turned this work over to Effie Spalding, Volney Spalding's wife (Spalding 1905).

[8] W. A. Cannon to D. T. MacDougal, 2 Dec 1903, AHS.

[9] W. A. Cannon to D. T. MacDougal, 17 May 1904, AHS.

[10] W. A. Cannon to D. T. MacDougal, 22 Feb 1905, AHS.

[11] W. A. Cannon to D. T. MacDougal, 15 Sep 1903, AHS.

[12] W. A. Cannon to D. T. MacDougal, 13 Jun 1904, AHS.

[13] W. A. Cannon to D. T. MacDougal, 18 Aug 1904, AHS.

[14] F. V. Coville to D. T. MacDougal, 12 Jul 1904, AHS.

[15] W. A. Cannon to D. T. MacDougal, 24 Oct 1904, AHS.

[16] F. V. Coville to W. A. Cannon, 3 Oct 1904, AHS.

[17] D. T. MacDougal to W. A. Cannon, 16 Aug 1905, AHS.

[18] W. A. Cannon to D. T. MacDougal, 21 Dec 1905, AHS.

[19] R. S. Woodward to W. A. Cannon, 1 Mar 1905, AHS.

[20] W. A. Cannon to R. S. Woodward, 8 Mar 1905, AHS.

[21] W. A. Cannon to D. T. MacDougal, 11 Jan 1911, AHS.

[22] Cannon was not the first scientist to investigate the root systems of desert plants: Preston had already excavated five cactus species near Tucson and discovered the heteromorphic root system characteristic of many cacti (Preston 1900).

[23] This method, which emphasized the horizontal spread of roots, may not have provided adequate information on their vertical profile. Weaver (1919), in excavating roots of prairie plants to depths of six meters, emphasized equally their vertical and horizontal distribution.

[24] Cannon's classification of cactus root systems relied on a limited number of species. Gibson and Nobel (1986), in classifying the root systems of North and South American cacti, found five common patterns.

[25] Yeaton et al. (1977) confirmed and extended Cannon's results. They demon-

strated effects of competition on plant size and discovered interspecific competition between several species pairs.

[26] Barbour challenged Cannon's conclusions about competition: Cannon's own data showed that "there may be considerable space between root systems as well as overlap of roots of close neighbors," he wrote (Barbour 1973, p. 46).

[27] D. T. MacDougal to W. A. Cannon, ca. Aug 1908, AHS.

[28] D. T. MacDougal to W. R. Dudley, 18 Nov 1910, AHS. The logical place to extend their work would have been northern Mexico, but political turmoil, culminating in the revolution of 1911, had made the border region unsafe for travelers.

[29] These censuses were simply tallies of individuals for each species present. The value of this data seems dubious as Cannon did not integrate it into his discussion of vegetation and environment. Plant censuses had been recently popularized by Clements (1905, 1907), and it seems likely that Cannon undertook them in the belief that they were a necessary and proper activity of plant ecologists.

[30] Cannon later noted that succulents reach their best development in regions of moderate rainfall, extending only a short distance into drier and wetter regions (Cannon 1924a). Their distribution, in other words, is correlated less with season of rainfall than total rainfall. This point has been corroborated with abundant detail by Burgess and Shmida (1988).

[31] W. A. Cannon to D. T. MacDougal, 3 May 1917, AHS.

[32] W. A. Cannon to D. T. MacDougal, 13 May 1916, AHS.

[33] D. T. MacDougal to G. Sykes, 13 Jul 1917, AHS.

[34] W. A. Cannon to D. T. MacDougal, 1 Jul 1918, AHS.

[35] W. A. Cannon to D. T. MacDougal, 22 Aug 1918, AHS.

[36] Cannon may have consciously or unconsciously borrowed this value of 0.15 inch from Forrest Shreve, who estimated that at the Desert Laboratory, "the lower limit of significant rainfalls may be placed at 0.15 in" (Shreve 1917, p. 21).

[37] Cannon oversimplified the problem of leaf reduction. Small leaves are more efficient than large ones in dissipating heat, thus are able to maintain temperatures closer to that of the air (Gates 1968; Gates et al. 1968). A major benefit of lowered leaf temperature for desert plants is reduced transpiration per unit of leaf area (Smith 1978).

[38] The topic of leaf morphology in relation to climate was then beginning to receive the attention of ecologists (Parkhurst and Loucks 1972). Cannon did not cite such contemporaries as Bailey and Sinnott (1916) or Brown (1919), presumably because he was unfamiliar with their work.

[39] Cannon may have taken this list of xeromorphic adaptations from Schimper (1903), who may in turn have gotten it from Volkens (Oppenheimer 1960).

[40] Although Vlamis and Davis (1944) call the oxygen studies presented in *Physiological Features of Roots* "indecisive," other colleagues cited the book frequently—for example, Weaver and Bruner (1927) and Miller (1938).

[41] W. A. Cannon to D. T. MacDougal, 9 Feb 1923, SC.

[42] D. T. MacDougal to W. A. Cannon, 13 Feb 1923, SC.

[43] D. T. MacDougal to W. A. Cannon, 30 Mar 1923, SC.

[44] W. A. Cannon to D. T. MacDougal, 4 Sep 1923, SC. According to Carnegie Institution records, he retired officially from the staff on 1 Jan 1925.

[45] During this period, at least some of his research was funded by the American Association for the Advancement of Science and the National Research Council.

[46] B. E. Livingston to F. Shreve, 2 Feb 1926, SC.

[47] Drew (1979) pointed out that root classification systems generally suffer from oversimplification, since environmental factors often override root morphology to such an extent that a given root system fails to conform to any of the classified types. Moreover, he noted that among ten types of root systems described for Near Eastern plants, none matched Cannon's types.

[48] Only Nobel (1988) has paid more than passing attention to Cannon's research, and he restricted himself to Cannon's work on cacti.

[49] W. A. Cannon to D. T. MacDougal, 21 Dec 1905, AHS.

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